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ARTICLE

THE SKULL OF *TELEOSAURUS CADOMENSIS* (CROCODYLOMORPHA; THALATTOSUCHIA), AND PHYLOGENETIC ANALYSIS OF THALATTOSUCHIA

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ABSTRACT—Several *Teleosaurus* skulls were described during the nineteenth century. Unfortunately, all skulls from this genus were destroyed during World War II. The only available skull is currently preserved in the MNHN. Thanks to a new preparation, new anatomical features can be seen, such as the morphology of the nasal cavity, the external otic recess, and the distribution of the foramina for the cranial nerves. A phylogenetic analysis is presented, including 14 thalattosuchian taxa. This analysis has generated four equally most parsimonious trees, where the thalattosuchians are closely related to the pholidosaurids and dyrosaurids, forming a longirostrine taxa. These relationships have been often considered to be based on homoplasies, related to the longirostrine morphology. This is also suggested herein, as the deletion of the longirostrine dependant characters or of the most longirostrine thalattosuchians in the analysis provide a consensus tree where thalattosuchians are basal crocodyliforms, a result more generally accepted. As the deletion of the most longirostrine thalattosuchians precludes the longirostrine problem in the phylogenetic analysis of Crocodyliformes, this deletion seems to be the less unsatisfactory solution to assess the crocodyliform relationships. The phylogenetic analysis also provides interesting information on the thalattosuchian relationships: *Teleosaurus* is the basal-most thalattosuchian, Teleosauridae is paraphyletic and *Pelagosaurus* is neither the basal-most thalattosuchian nor the basal-most metriorhynchid. The metriorhynchid relationships support previous works, as '*Teleidosaurus*' is paraphyletic and the basal-most metriorhynchid, *Metriorhynchus* is more closely related to other metriorhynchid than '*Teleidosaurus*,' and *Enaliosuchus*, for which the relationships are tested for the first time, is the sister taxon of *Dakosaurus*. *Geosaurus* is the sister taxon of the clade *Dakosaurus* + *Enaliosuchus*.

INTRODUCTION

The thalattosuchians are marine crocodyliforms present in nearly all continents. Most are longirostrine forms with anteroposteriorly elongate supratemporal fenestrae. *Teleosaurus*, unlike most other longirostrine thalattosuchians, has short and nearly as wide as long supratemporal fenestrae. This genus has been often reported from the Jurassic of France (Cuvier, 1824; Eudes-Deslongchamps, 1864, 1867–1869, 1896; Geoffroy Saint-Hilaire, 1825; Sauvage, 1874) and Great Britain (Owen, 1841). Two specimens from China have also been referred to this genus, but the rostrum reported by Young (1964) should be referred to *Peipehsuchus*, and the osteoderms described by Liu (1961) from the same formation, may belong to the same genus.

The genus *Teleosaurus* was erected by Geoffroy Saint-Hilaire (1825) for *Crocodilus cadomensis* Lamouroux 1820. Several species have been described later such as *T. gladius* (Eudes-Deslongchamps, 1868), *T. subulidens* (Phillips, 1871), and *T. geoffroyi* (Eudes-Deslongchamps, 1868). Specimens referred to *T. gladius* were all destroyed in Caen during the Second World War, but Vignaud (1995) proposed synonymy between *T. gladius* and *T. cadomensis* based on the description by Eudes-Deslongchamps (1868). The mandibular fragment attributed to *T. subulidens* is also reported to *T. cadomensis* (Vignaud, 1995). Only *T. geoffroyi*, described on mandibular fragments destroyed in Caen in 1944 (Eudes-Deslongchamps, 1868), is the second species considered as a valid species by Vignaud (1995).

The skull studied herein has been often described and figured (Cuvier, 1824; Geoffroy-Saint-Hilaire, 1825; Blainville, 1855; Gervais, 1859; Eudes-Deslongchamps, 1868; Morel de Glasville, 1876, 1880), but thanks to a tidy preparation, the bones and the organization of the endocast are available. All other *Teleosaurus* skulls described by Eudes Deslongchamps (1869) were destroyed during the Second World War. The holotype also seems to be lost, but as apparently some remains were saved but are still unavailable, it is not possible to be sure that the holotype is lost or 'survived' at least partially. For the present, if its survival is unlikely, it is not possible to create a neotype. So, the present specimen is the only skull of this genus available, hence its particular importance.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, USA; **CNRS**, Centre National de la Recherche Scientifique, Paris, France; **CNRST**, Centre National de la Recherche Scientifique et Technologique, Mali; **IRSNB**, Institut Royal des Sciences Naturelles, Bruxelles, Belgium; **LGBPH**, Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Université de Poitiers, France; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **NHM**, Natural History Museum, London, United Kingdom; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **SUNY**, State University of New York, Stony Brook, USA.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
THALATTOSUCHIA Fraas, 1901
TELEOSAURUS Geoffroy, 1825
TELEOSAURUS CADOMENSIS (Lamouroux, 1820)
(Figs. 1–5)

Crocodilus cadomensis Lamouroux, 1920: 160-163.
'Gavial de Caen' Cuvier, 1824: 127, pl. 7, figs. 1–5, 10.
'*teleosaurus codomensis*' Bornet, 1866: 436-439.
Teleosaurus gladius Eudes-Deslongchamps, 1868: 326.
Teleosaurus subulidens Phillips, 1871: 184–194, fig. 54.

Holotype—A complete skull noted by Lamouroux (1820), and described by Geoffroy Saint Hilaire (1825).

Referred Specimen—MNHN AC 8746, a quarter of a skull, first figured by Cuvier (1824).

Horizon and Locality—Bathonian of Allemagne, 3 km in south of Caen, Normandy, France.

Emended Diagnosis—Snout narrow, broadening abruptly at orbits; 45-55 maxillary teeth; 50-60 dentary teeth; some teeth are located higher on the maxilla in lateral view (1 on 3); supratemporal fenestra nearly as wide as long; choana wider than palatines between the suborbital fenestrae.

DESCRIPTION

State of Preservation—Only the left half of the skull is preserved, and the snout is missing (Fig. 1). Further preparation of skull allows a complete description of the braincase and its various cranial nerve openings.

Cranial Openings—The antorbital fenestra is a thin slot, elongated anteroposteriorly between the lacrimal and maxilla (Fig. 1). It is bordered ventrally by the maxilla and dorsally by the lacrimal. Medially, it opens in the postnasal cavity.

The orbit is circular in shape, and oriented more dorsally than laterally (Fig. 1). Its anterior margin is comprised of lacrimal. The ventral margin is mainly formed by the jugal, the postorbital participating in the posteroventral margin. The frontal forms the posteromedial quarter of the margin, the postorbital forms the posterolateral margin, and the anterior portion of the medial margin is formed by the prefrontal. The interorbital space would have to be narrow.

The posterior wall of the antorbital cavity is exposed. The postnasal fenestra, which pierces the antorbital wall, enables a communication between the antorbital cavity (sensu Witmer, 1995) and the suborbital cavity. It is bordered lateroventrally by the lacrimal and dorsolaterally and dorsally by the prefrontal. The prefrontal and lacrimal forms a high transverse lamina forming the anterior wall of the orbit. The prefrontal pillar forms the medial margin of the postnasal fenestra to which the palatine participates ventrally. The prefrontal pillar is lateromedially extended, and bears an anteroposterior lamina in its dorsalmost portion in the antorbital cavity. The maxilla forms the ventral margin of the postnasal fenestra.

The supratemporal fenestra is large, nearly as wide as long with straight margins (Fig. 1). The corners are rounded. The postorbital forms two-thirds of the anterior margin, and the remainder is formed by the frontal, which forms the anteriormost third of the interfenestral bar. The squamosal forms one-quarter of the lateral margin, whereas it participates in half of the posterior one. The parietal forms two-thirds of the interfenestral bar and half of the posterior margin. The interfenestral bar is moderately wide and ornamented. The posterior margin of the supratemporal fenestra is a thin crest, and the lateral margin is strongly laterally sloped.

The temporal canal is a foramen elongated lateromedially, bordered dorsally half by the squamosal and parietal, and ventrally by the prootic. The quadrate participates very slightly to the lateroventral margin.

The infratemporal fenestra is triangular in shape, twice longer than high and bordered dorsally by the postorbital on three-quarters (Fig. 2B). The quadrate participates to the posterodorsal margin, and the quadratojugal to the posteroventral margin. The jugal forms more than three-fourths of the lower bar, the quadratojugal forming the remain.

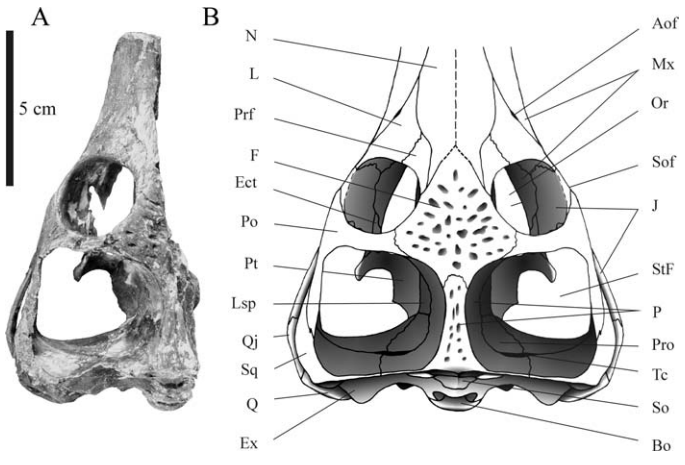

FIGURE 1. *Teleosaurus cadomensis*, MNHN AC 8746, from the Bathonian of France. Skull in dorsal view. **Abbreviations**: **Aof**, anteorbital fenestra; **Bo**, basioccipital; **Ect**, ectopterygoid; **Ex**, exoccipital; **F**, frontal; **J**, jugal; **L**, lacrimal; **Lsp**, laterosphenoid; **Mx**, maxilla; **N**, nasal; **Or**, orbit; **P**, parietal; **Po**, postorbital; **Prf**, prefrontal; **Pro**, prootic; **Pt**, pterygoid; **Q**, quadrate; **Qj**, quadratojugal; **So**, supraoccipital; **Sof**, suborbital fenestra; **Sq**, squamosal; **Stf**, supratemporal fenestra; **Tc**, temporal canal.

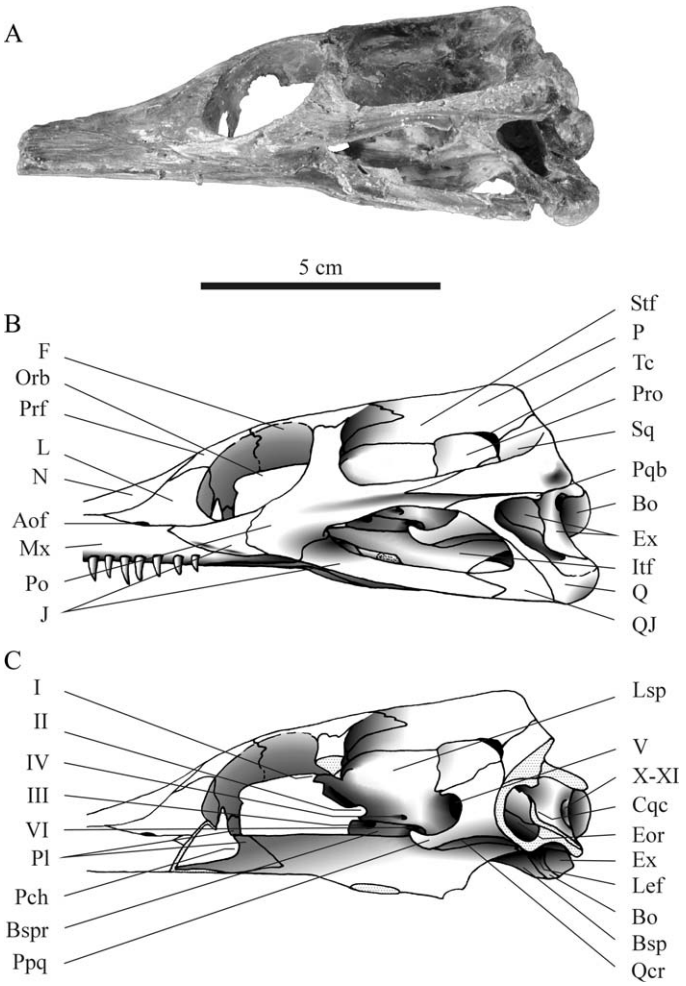

FIGURE 2. *Teleosaurus cadomensis*, MNHN AC 8746, from the Bathonian of France. Skull in lateral view. **Abbreviations**: **Aof**, anteorbital fenestra; **Bo**, basioccipital; **Bsp**, basisphenoid; **Bspr**, basisphenoid rostrum; **Cqc**, cranioquadrate canal; **Eor**, external otic recess; **Ex**, exoccipital; **F**, frontal; **Itf**, infratemporal fenestra; **J**, jugal; **Lef**, lateral eustachian foramen; **Lsp**, laterosphenoid; **Mx**, maxilla; **Orb**, orbit; **P**, parietal; **Pch**, primary choana; **Pl**, palatine; **Po**, postorbital; **Ppq**, pterygoid process of quadrate; **Pqb**, posterior quadrate bulge; **Prf**, prefrontal; **Pro**, prootic; **Pt**, pterygoid; **Q**, quadrate; **Qcr**, quadrate crest; **Stf**, supratemporal fenestra; **Tc**, temporal canal; **I**, foramen for the olfactory nerve; **II**, foramen for the optic nerve; **III**, foramen for the occulomotor nerve; **IV**, foramen for the trochlear nerve; **V**, foramen for the trigeminal nerve; **VI**, foramen for the abducens nerve; **X-XI**, foramen for cranial nerve X-XI.

The otic aperture is well preserved. It is bordered anteriorly and dorsally by the quadrate and posteriorly by the exoccipital, but the posterior margin is not completely closed (Fig. 2). The posterior lamina of the exoccipital, forming the posterior margin of the otic aperture, is not sutured dorsally with the posterodorsal portion of the quadrate, but separated from it by a narrow slit. This lamina separates the otic aperture from the cranioquadrate canal.

The posttemporal fenestra is a thin slot, elongated lateromedially (Fig. 3). It is bordered dorsally by the parietal, and ventrally by the supraoccipital.

The foramen magnum is large, mainly surrounded by the exoccipital, the basioccipital forming only a small part of its ventral margin (Fig. 3).

The suborbital fenestra is small, elongated anteroposteriorly, with rounded anterior and posterior margins, the anterior margin being narrower than the posterior one (Fig. 4). The palatine forms its medial margin, the maxilla its anterior and half of the lateral margin and the pterygoid the posterior one. The ectopterygoid participates to less than half of the posterolateral margin. The anterior margin of the suborbital fenestra reachs the level of the last maxillary alveoli.

The choana is widely opened, without septum (Fig. 4). Its anterior margin is formed by the palatine, and the pterygoid forms the lateral and posterior margins. The ventral surface of the pterygoid is deeply concave dorsally in the choana.

Maxilla—The maxilla is smooth, without or with light ornamentation (Figs. 1, 2). It forms the anterior, posterior, and the ventral margin of the antorbital fenestra. Ventrally, the maxilla bears small, circular, and closely set alveoli. The tooth row is widely separated from the lateral margin of the suborbital fenestra by a wide and smooth medial palatal lamina. This lamina is projected far posteriorly, and reduces strongly the participation of the ectopterygoid in the lateral margin of the suborbital fenestra.

In medial view, the maxilla is pierced by two foramina in the antorbital cavity (Fig. 5). The first, located immediately anterior to the antorbital fenestra, is bordered dorsally and medially by the lacrimal, and laterally by the maxilla. Following Witmer (1997), it is probably the paranasal cavity. It is weakly extended anteriorly, as it is not seen in the anterior broken portion of the snout. The second foramen, below and slightly anterior to the first one, could be the passage for the maxillary nerve. This aperture is completely enclosed by the maxilla, and the dorsal margin of the foramen is posteriorly prolonged by a thin crest, which reach posteriorly the lacrimal, in the base of the lateroventral margin of the anterior wall of the orbit (or lateroventral

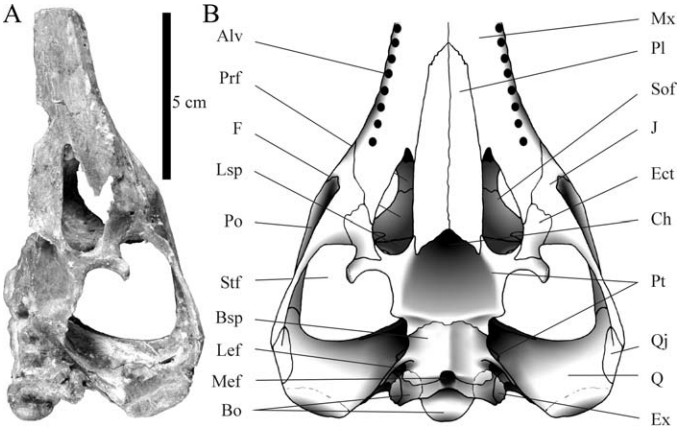

FIGURE 4. *Teleosaurus cadomensis*, MNHN AC 8746, from the Bathonian of France. Skull in ventral view. **Abbreviations**: **Alv**, alveolus; **Bo**, basioccipital; **Bsp**, basisphenoid; **Ch**, choana; **Ect**, ectopterygoid; **Ex**, exoccipital; **F**, frontal; **J**, jugal; **Lef**, lateral eustachian foramen; **Lsp**, laterosphenoid; **Mef**, medial eustachian foramen; **Mx**, maxilla; **Pl**, palatine; **Po**, postorbital; **Prf**, prefrontal; **Pt**, pterygoid; **Q**, quadrate; **Qj**, quadratojugal; **Sof**, suborbital fenestra; **Stf**, supratemporal fenestra.

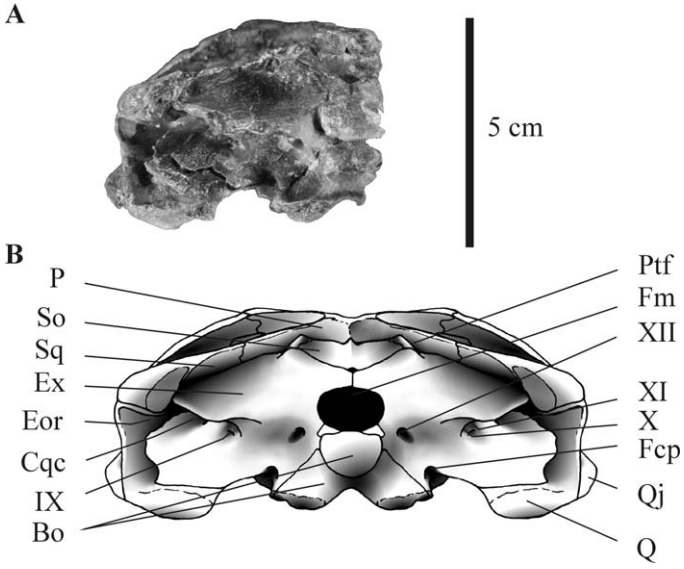

FIGURE 3. *Teleosaurus cadomensis*, MNHN AC 8746, from the Bathonian of France. Skull in occipital view. **Abbreviations**: **Bo**, basioccipital; **Cqc**, cranioquadrate canal; **Eor**, external otic recess; **Ex**, exoccipital; **Fm**, foramen magnum; **Fcp**, foramen caroticum posterius; **P**, parietal; **Ptf**, posttemporal fenestra; **Q**, quadrate; **Qj**, quadratojugal; **So**, supraoccipital; **Sq**, squamosal; **X-XII**, foramina for cranial nerves.

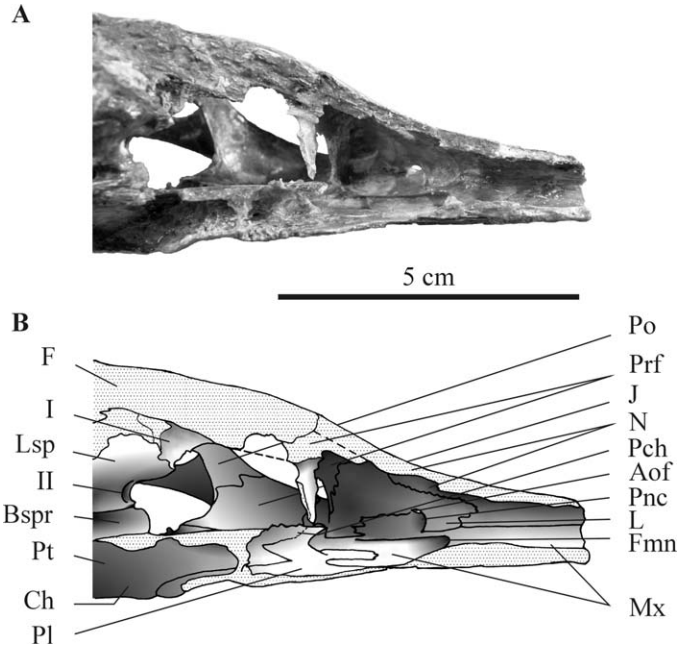

FIGURE 5. *Teleosaurus cadomensis*, MNHN AC 8746, from the Bathonian of France. Skull in medial view. **Abbreviations**: **Aof**, anteorbital fenestra; **Bspr**, basisphenoid rostrum; **Ch**, choana; **F**, frontal; **Fmn**, foramen for the maxillary neurovasculature; **J**, jugal; **L**, lacrimal; **Lsp**, laterosphenoid; **Mx**, maxilla; **N**, nasal; **Pch**, primary choana; **Pl**, palatine; **Pnc**, paranasal cavity; **Po**, postorbital; **Prf**, prefrontal; **Pt**, pterygoid; **I**, foramen for the olfactory nerve; **II**, foramen for the optic nerve.

margin of the postnasal fenestra). This canal is triangular in cross section (also visible in the anterior view of the broken snout).

Nasal—There are two nasals, very weakly ornamented with light furrows (Fig. 1). They are widely separated posteriorly by the anterior process of the frontal, and the posterior processes thus approach the medial margin of the orbits. The posterior process of the nasal is strongly extended posteriorly, and reaches the level of the mid-length of the orbit.

Lacrimal—The lacrimal is relatively large and forms the anterior margin of the orbit (Fig. 1). It is half longer than the prefrontal, and half longer than wide. The lacrimal forms the dorsal margin of the small antorbital fenestra, and the lateroventral margin of the postnasal fenestra. It also forms the medial margin of the paranasal cavity. There is no nasolacrimal canal.

Prefrontal—The prefrontal is small, short, and narrow (Fig. 1). It is less than twice longer than wide. It forms the dorsal portion of the prefrontal pillar. The ventral portion of the prefrontal pillar is broken, but a portion of the palatine is still sutured to the prefrontal. The prefrontal forms the dorsomedial, the dorsal, and most of the lateral margin of the postnasal fenestra.

Frontal—The anterior process of the frontal is not preserved, but seems to have been short (Fig. 1). It extends anteriorly between the posterior processes of the nasals, and its contact with the prefrontal is extremely reduced on the skull roof. It contacts the postorbital laterally, and forms less than half of the posterior margin of the orbit. The frontal participates largely in the interfenestral bar posteriorly. Within the supratemporal fenestra, on its medial surface, the frontoparietal suture is first posteroventrally oriented on one centimetre, then it is directed anterolaterally to reach the postorbital. Thus, there is no contact between the frontal and the laterosphenoid, both being separated by the parietal. Anteriorly, in the interorbital space, the frontal is high, and its ventral margin bears a dorsal sulcus elongated craniocaudally for the passage of the olfactory nerve (I) (Fig. 2C). The frontal is ornamented dorsally with shallow but widely spaced pits.

Jugal—The jugal forms the ventral margin of the orbit (Fig. 2B). It is as extended as the prefrontal anteriorly, and its contact with the lacrimal is as long as the contact between the maxilla and the lacrimal. On the posteroventral margin of the orbit, the postorbital covers completely the lateral margin of the jugal, which is not visible at this level. The jugal forms the anteroventromedial portion of the postorbital bar, which is indistinct from the dorsal margin of the postorbital. Posterior to the postorbital bar, the dorsal margin of the jugal is medially displaced in relation to the lateral margin of the jugal in this bar (see below). The posterior process of the jugal is lateromedially flattened and forms most of the ventral margin of the infratemporal fenestra. Posteriorly, the posterior process covers slightly the quadratojugal laterally, and ends in front of the posterior margin of the infratemporal fenestra. Its dorsal and ventral margins are straight. In ventral view, the jugal reaches the level of the last maxillary tooth, laterally to the maxilla (Fig. 4). The jugal should not have to participate in the lateral margin of the suborbital fenestra, but as this part is laking, it is not possible to be certain. Its medial process covers significantly the ectopterygoid dorsally, and bears a posterolateral process dorsal to this bone which almost contacts the pterygoid.

Quadratojugal—The quadratojugal is widely exposed posterior to the jugal and does not reach the quadrate condyle (Fig. 2B). It forms the posteroventral corner of the infratemporal fenestra, and participates in its posteroventral and posterodorsal margins.

Postorbital—The postorbital forms most of the posterior margin of the orbit, and contributes to half of its ventral margin with a ventrolateral process (Fig. 1, 2B). This process covers completely the jugal laterally at the level of the postorbital bar. The postorbital bar is triangular in cross section, its lateral margin being slightly convex, the posteromedial being strongly concave, more than the anteromedial. The postorbital bar is not distinct from the orbital margin, and the jugal forms its medial portion. The postorbital bar is indistinct from the dorsal margin of the postorbital, which forms nearly the whole of the bar. The posterodorsal process forms most of the lateral margin of the supratemporal fenestra, and extends to the level of the anterior margin of the external otic recess (Fig. 2). This process is divided in two parts by the anterior process of the squamosal, in a posteromedial and a posteroventral process. The postorbital forms three-quarters of the dorsal margin of the infratemporal fenestra, and its posteroventral process extends between the anterolateral process of the squamosal and the anterior process of the quadrate. The postorbital is exposed in ventral view, lateral to the jugal.

Parietal—The parietal forms most of the interfenestral bar, and bears an anteroventrolateral process between the frontal and the laterosphenoid that reachs the postorbital (Figs. 1, 2C). Ventrally, the parietal broadly contacts the laterosphenoid, and the prootic posteriorly, but does not contact the quadrate. It participates in half of the mediodorsal margin of the temporal canal. The dorsal margin of the parietal is slightly ornamented with shallow pits, and would have comprised half of the posterior margin of the supratemporal fenestra. It participates in the occipital surface, and forms a high rectangle above the supraoccipital, being wider than this latter bone. Its occipital portion bears a small dorsoventral medial crest (Fig. 3).

Squamosal—The squamosal contributes to half of the posterior margin of the supratemporal fenestra (Fig. 1). It sends off an anterolateral process on the postorbital, and forms half of the laterodorsal margin of the temporal canal. In lateral view, the squamosal contacts the quadrate posteroventrally, and does not participate in the infratemporal fenestra (Fig. 2B). In the occipital surface, the squamosal forms the low dorsolateral corner (Fig. 3), that is strongly posteroventrally inclined, forming an acute angle with the exoccipital surface.

Supraoccipital—The supraoccipital is triangular shaped, located below the parietal (Fig. 3). It is a small bone separated from the foramen magnum by the exoccipitals. It bears two lateral small posterior tuberosities, below the posttemporal fenestrae.

Exoccipital—The exoccipitals form most of the occipital surface, contributing slightly to each lateral sides of the occipital condyle, and surrounding more than three-quarters of the foramen magnum (Fig. 3). Below the posttemporal fenestra, the exoccipital participates slightly in the ventrolateral margin of the small tuberosity. Laterally, it constitutes the ventral portion of the robust paroccipital process, and surrounds posteriorly, ventrally and anteroventrally the cranioquadrate canal. The paraoccipital processes are long, thin plates that have become deflected into the horizontal plane; this rotation causes the ventral margin to form a prominent ridge that overhangs the quadrate. A significant gap exists between the paraoccipital process and the quadrate. The paroccipital process does not seem to be sutured to the squamosal laterally, but only in simple contact (not actually fixed to each other). The exoccipital bears a thin lamina posterior to the external otic recess, that approaches dorsally the bulge of the posterodorsal process of the quadrate (Fig. 2). This lamina forms the posterior margin and part of the medioventral margin of the external otic recess. The anterior margin of the cranioquadrate canal is thus incompletely separated from the external otic recess. Ventrally, the exoccipital participates ventrolaterally in the basioccipital tuber, in a wide ventral process, and borders the posterior margin of the lateral eustachian foramen (Fig. 4). The foramen for the hypoglossal nerve (XII) is small, and lateroventrally oriented on the exoccipital. It is located at the same level as the floor of the foramen magnum. The foramen caroticum posteriorus is wide and very low on the ventral process of the exoccipital, not far from the

ventral margin of the basioccipital tuberosity, and oriented ventroposteriorly. A group of three foramina is located ventromedially to the exit of the cranioquadrate canal. The intraspecific variability of this foramina seems to be large (Broin, 1965; Vignaud, 1995) and their interpretation difficult (Wenz, 1968). It is based herein on comparison with other crocodyliformes. The vagus (X) and accessory (XI) nerves, even if they are separated, exit through a common opening, close from the glossopharyngeal (IX) nerve. The later foramen lies slightly ventromedially to the vagus and accessory foramina. All are small, located far laterally from the foramen for nerve XII.

Quadrate—The condylar part of the quadrate is oriented posteroventrally (Fig. 3). The quadrate contacts the squamosal lateral to the temporal canal, and the postorbital more anteriorly, in the supratemporal fenestra. It has no contact with the parietal, but contacts extensively the prootic from the dorsal margin of the trigeminal foramen (V) to the lateroventral margin of the temporal canal (Fig. 2C). It bears a long anteroventral process between the laterosphenoid and the pterygoid, that extends between the basisphenoid and the pterygoid but does not contact them in its anteriormost portion. So, it is not sutured anteriorly with the laterosphenoid, the basisphenoid, or the pterygoid, and appears to have been isolated from direct contact with these elements. It extends anteriorly at the level of the foramen for the cranial nerve VI on the basisphenoid. This process bears a strong ventral crest that extends posterolaterally on the body of the quadrate. This crest divides the ventral margin of the quadrate in two parts: the dorsalmost forming the posterior wall of the supratemporal fenestra, oriented and convex anteriorly; and a ventral part, convex dorsally, forming a deep medioventral concavity (Fig. 2C, 4). This concavity disappears progressively posterolaterally with the disappearance of the crest on the ventral margin of the condylar part of the quadrate. At this level, the anterodorsal and the ventral portions of the quadrate are not separated by a crest, but both are concave continuously anteroventrally. In lateral view, the quadrate contributes to the posterior margin of the infratemporal fenestra, and its anterodorsal process tapers anteriorly, separated from the squamosal by the posteroventral process of the postorbital (Fig. 2B). The posterodorsal process of the quadrate contacts the squamosal dorsally, bears a small ventral bulge in its posteriormost portion, and forms the anterior and dorsal margins of the external otic recess. The small bulge forms the anterodorsal margin of the cranioquadrate canal (Fig. 2B).

Palatine—The palatine forms the ventral lamina of the duct for the internal naris (Fig. 4). Its anteriormost portion is missing, but its print on the maxilla is preserved, thus it largely extends anteriorly beyond the anterior margin of the suborbital fenestra to reach the same level as the lacrimal. Anteriorly, the palatine covers ventrally the maxilla, and forms the anterior margin of the internal naris posteriorly. The palatine participates shortly in the lateral margin of the nasal duct anteriorly (Fig. 2C). Thus, it forms the lateral margin of the primary choana in the antorbital cavity, and its anterior margin is strongly concave posteriorly (Fig. 5). The narial duct ends in the primary choana (sensu Witmer, 1995) immediately anterior to the prefrontal pillar. It seems to have borne a dorsal process, which formed the ventral portion of the prefrontal pillar.

Pterygoid—The pterygoid is well extended craniocaudally (Fig. 4). Anteriorly, it forms the lateral and the dorsal wall of the narial duct (Fig. 2C). It participates in the lateral and posterior margins of the choana. It forms the posterior margin of the suborbital fenestra, and participates in its posterolateral and posteromedial margins. The lateral wing of the pterygoid is small, and partly covered ventrally by the ectopterygoid. It forms a short and high torus transiliens, projected dorsally and posteriorly. Because of this posterior projection, the posterior margin of this wing is strongly concave anteriorly. Its posteriormost lateral margin is straight, but should have borne a small lateral process. The pterygoid forms a posterolateral process between the quadrate and the basisphenoid that exceeds the level of the lateral eustachian foramina.

Ectopterygoid—The ectopterygoid is small, participates posterolaterally in the suborbital fenestra, and covers ventrally the lateral portion of the pterygoid (Fig. 4). It should have to contact the maxilla anteriorly.

Basioccipital—The basioccipital forms most of the robust and rounded occipital condyle (Fig. 3). The basioccipital tubera are visible ventral to the occipital condyle in occipital view. The area between the basioccipital tubera and the occipital condyle is slightly arched dorsally, the short posterior margin of the basioccipital tubera being nearly vertical. The two basioccipital tubera are separated by a deep dorsal sulcus. In ventral view, the basioccipital is relatively thin medially between the basioccipital tubera (just posterior to the medial eustachian foramen). The narrow medial part of the basioccipital separates the tubera which are tear-drop shaped in ventral view. The posterolateral part of the tuber is located more dorsal than its medial part. The basioccipital is visible in lateral view as a thin wedge between the basisphenoid and the exoccipital, its dorsal margin tapering to contact slightly the lateral eustachian foramen (Fig. 2C).

Laterosphenoid—The laterosphenoid is located ventral to the frontal and the parietal, and does not contact the squamosal (Fig. 2C). Its ventral contact with the basisphenoid rostrum lies at the same level as the trigeminal foramen (V). Anteriorly, it is expanded laterally below the frontal and contacts the postorbital. Its anterior margin (capitate process) is directed laterally. The laterosphenoid does not contact the frontal in the supratemporal fenestra, but is separated from this bone by the parietal. The contact with the parietal is large, but this with the postorbital seems to be small. The suture with the parietal is linear, parallel compared to the skull roof (dorsal limit of the interfenestral bar). Opposite laterosphenoids meet each other sagittaly below the olfactory foramen (I), and below expands slightly around the optic foramen (II). A sharp and short laterosphenoid process is present anteroventral to the optic foramen, sutured to the dorsal margin of the basisphenoid rostrum. The posterior suture between the laterosphenoid and the prootic is vertical and in relief. Posteroventrally, the laterosphenoid forms the anteromedial margin of the trigeminal nerve. There is not a distinct laterosphenoid foramen for the ophthalmic branch of the trigeminal nerves (V_1), but a shallow anteroposterior groove prolongs the trigeminal foramen, indicating the external pathway of the ophthalmic branch. Anteriorly, the laterosphenoid is pierced by the foramen for the trochlear nerve (IV), prolonged anteriorly by a shallow groove. Anterior to the trigeminal foramen, the laterosphenoid expands laterally, indicating the presence of the cerebellum.

Basisphenoid—The basisphenoid is long and widely exposed anterior to the medial eustachian foramen in ventral view, and forms the anterior margin of this foramen (Fig. 4). It bears a long posterolateral process, and forms the anterior and lateral margins of the lateral eustachian foramen, which is located dorsally, at the top of the lateral exposure of the basioccipital. Posterodorsally, the basisphenoid makes short contact with the quadrate, separated from it by the posterior process of the pterygoid. Anteriorly, the basisphenoid rostrum is not high, but moderately elongated, and sutured dorsally with the laterosphenoid (Fig. 2C). It is pierced anteriorly by the wide foramen for the oculomotor nerve (III), immediately below the laterosphenoid-basisphenoid suture, and posterior to the level of the opening for the optic nerve (II). It is directed anteriorly. Ventrally, the basisphenoid rostrum is sutured with the pterygoid, and extends posteriorly nearly at the same level as the laterosphenoid-prootic suture. Ventral to the basisphenoid-laterosphenoid contact, a small foramen, probably for the abducens nerve (VI),

pierces the basisphenoid at the same level as the anterior process of the pterygoidian ramus of the quadrate. The right portion of the skull is lacking, and the eustachian system is exposed. The medial eustachian foramen opens between the basioccipital and the basisphenoid in a short tube that bifurcates dorsally into an anterior and posterior basicranial tube, situated within the basisphenoid and basioccipital, respectively. The posterior tube divides in a right and left fork immediately dorsal to the bifurcation of the basicranial tube in a posterior and anterior portion. The anterior tube, enclosed within the basisphenoid, is also divided anteriorly in a left and right rami. The hypophysial fossa is completely enclosed in the basisphenoid.

Prootic—The prootic is widely exposed on the lateral margin of the braincase and on the posterior wall of the supratemporal fenestra (Fig. 2C). It is excluded from the margin of the trigeminal nerve by the quadrate and the laterosphenoid, and forms the ventral margin of the temporal canal.

DISCUSSION

Comparison

Because the specimens of *T. geoffroyi*, the other *Teleosaurus* species recognised as valid (Vignaud, 1995), are only mandibular or snout material, comparison with the present specimen of *T. cadomensis* is not possible. Thus, the comparison will only be provided with other genera. The specimen described by Eudes Deslongchamps (1869) is also used in comparison to build the emended diagnosis. Most of the characters used in the diagnosis are from Vignaud (1995).

The snout of *T. cadomensis* is narrow, and broadens abruptly at orbits, whereas the snout broadens gradually in other thalattosuchians. The number of maxillary and dentary teeth is particularly high, and higher than in other thalattosuchians. The position of the maxillary teeth is particular, and seems to differ between *T. cadomensis* and *T. geoffroyi*. In the latter, as in other thalattosuchians, the teeth have a linear arrangement, whereas one tooth of three is located higher on the maxilla in lateral view in *T. cadomensis* (Eudes-Deslongchamps, 1869; Vignaud, 1995). *T. cadomensis* also has a short supratemporal fenestra, that is nearly as wide as long. This fenestra is much longer than wide in other thalattosuchians, except in *Steneosaurus bollensis* where it is only slightly longer than wide (Westphal, 1962). The choana of *T. cadomensis* is very wide in the pterygoids, wider than the palatines between the suborbital fenestra. In other thalattosuchians, the choana is nearly as wide as the palatines. *T. cadomensis* differs from *Pelagosaurus* in having its orbits directed dorsally, the lateral margins of its supratemporal fenestrae smooth, and narrower nasals. It differs from *Pelagosaurus* and *Steneosaurus* in having the posterior margin of its choana located at the level of the pterygoid-basisphenoid suture (except in *S. bollensis* where the condition is similar to that observed in *Teleosaurus*; Westphal, 1962), the anterior margin of the choana is located posteriorly to the posterior quarter of the suborbital fenestra, and the posterior portion of its basisphenoid does not bear a strong anteroposterior crest (except in *S. bollensis* where the condition is similar to that observed in *Teleosaurus*; Westphal, 1962). Metriorhynchids have larger alveoli relative to skull size, wider nasals and interorbital space, a shorter snout, and a larger prefrontal (except in *Teleidosaurus*).

The specimen described herein has been previously extensively compared to the other thalattosuchians, but new preparation enables access to previously unknown characters.

As observed in other thalattosuchians, the antorbital fenestra is reduced to a thin slot located beneath the lacrimal as in *Pelagosaurus* and *Steneosaurus* (Eudes-Deslongchamps, 1869). In *Teleosaurus* (Fig. 2B), as in *Steneosaurus*, the antorbital fenestra is not prolonged anteriorly by a groove as in *Metriorhynchus* (Wenz, 1968), *Geosaurus* (Broili, 1932), and *Dakosaurus* (Gasparini et al., 2005). Around the antorbital fenestra, many crocodyliforms bear an antorbital fossa. The anterior groove observed in previously cited metriorhynchids has been interpreted as the antorbital fossa by Witmer (1997), who also suggested that the antorbital fossa was 'internalized,' or closed laterally, to form the paranasal cavity in *Pelagosaurus*. The same may be true in *Teleosaurus*, where the antorbital fossa is absent.

Medially, the relation between the antorbital fenestra and the paranasal cavity differs from that observed in other thalattosuchians where it is known. In *Pelagosaurus*, the paranasal cavity is separated from the nasal cavity by a thin wall of the maxilla, whereas *Metriorhynchus* lacks the paranasal cavity (Witmer, 1997). In *Teleosaurus*, the paranasal cavity is separated from the nasal cavity by a lacrimal wall (Fig. 5B). The foramen for the maxillary nerve and vessels is immediately posterior to the paranasal cavity in *Pelagosaurus* (Witmer, 1997), whereas in *Teleosaurus* it is located much more ventral, on the ventral floor of the nasal cavity. In living species, such as *Crocodylus niloticus*, this foramen is nearly as wide as the aperture of the caviconchal recess. It is very large in *Teleosaurus*, whereas the foramen described by Witmer (1997) in *Pelagosaurus* seems to be too small for maxillary nerve and vessels. So, a reexamination of *Pelagosaurus* is needed, to be sure that a second foramen does not exist in the ventral margin of the nasal cavity, as in *Teleosaurus*.

Contrary to Eudes-Deslongchamps (1869), the auditory region varies within thalattosuchians. The cranioquadrate canal is incompletely separated from the external auditory aperture by a thin ventral lamina of the exoccipital not closed dorsally in *Teleosaurus cadomensis* (Fig. 2C), a condition also observed in *Steneosaurus larteti* (MNHN 1885-28), *Pelagosaurus typus* (NHM 32599; MNHN 1914-9-9), and *Steneosaurus bollensis* (NHM R1999). The condition differs in *Mystriosaurus* cf. *bollensis*, *Metriorhynchus*, *Geosaurus*, *Dakosaurus*, *Teleidosaurus*, and *Enaliosuchus*, since the cranioquadrate canal is clearly separated from the otic aperture by the quadrate or exoccipital (due to the preservation, distinction is not always possible) and squamosal, these two bones being sutured (Eudes-Deslongchmaps, 1869; Andrews, 1913; Schroeder, 1922; Broili, 1932; Telles-Antunes, 1967; Wenz, 1968, 1970; Gasparini and Chong Diaz, 1977; Gasparini et al., 2005).

The organization of the braincase bones is nearly similar in *Metriorhynchus*, *Pelagosaurus*, and *Teleosaurus*, but differs from the condition observed in *Steneosaurus* (MNHN 1885-28, LGBPH LPPM 21). The basisphenoid rostrum is short, and its posterior margin extends posteriorly beyond the level of the anterior margin of the pterygoid ramus of the quadrate in *Metriorhynchus* (Wenz, 1968, 1870), *Pelagosaurus* (NHM 32599), *Teleosaurus* (Fig. 2C), and *Steneosaurus* (MNHN 1885-28, LGBPH LPPM 21). In the latter, the braincase, comprised of basisphenoid rostrum and laterosphenoid, is extensively elongated (Morel de Glasville, 1876, 1880). This disposition and 'stretching', is probably due to the extreme elongation of the postorbital part of the skull. This elongation is maximal in the forms with the most elongated supratemporal fenestrae. The same phenomenon is observed in the dyrosaurids, where the endocast is elongated in the forms with the longest supratemporal fenestrae, such as *Dyrosaurus phosphaticus* (Jouve, 2005) and *Rhabdognathus* sp. (Langston, 1995).

The organization of the cranial nerves differs between the species, and as previously noted, the organization described by Wenz (1968) and Telles-Antunes (1967) is probably erroneous (Jouve, 2004, 2005). The lower foramen described as for cranial nerve IV by Telles-Antunes (1967) is probably the foramen for the cranial nerve VI, and his III is probably the IV. In *Metriorhynchus*, the foramen described as for cranial nerve V_1 (Wenz 1968, 1970; Vignaud 1995), is probably for the cranial nerve IV. So, in the thalattosuchians, a laterosphenoid bridge separating

the ophthalmic branch (V_1) from the other branches of the trigeminal nerve does not seem to exist. The foramen for cranial nerve III differs in *Teleosaurus cadomensis*, *Steneosaurus*, and *Pelagosaurus typus*. In the latter, the right and left nerves III exit through a common foramen in the basisphenoid dorsal to the basisphenoid rostrum. The foramen separates the dorsal margin of the rostrum from the ventral margin of the laterosphenoid. In *Teleosaurus cadomensis*, the right and left nerve III exit through two foramina in the basisphenoid, separated by the dorsal margin of the basisphenoid rostrum. The anterodorsal margin of the basisphenoid rostrum contacts the ventral margin of the laterosphenoid (Fig. 2C). The right and left nerve III also exit through two foramina in *Steneosaurus*, and is located far posterior to the anterior margin of the basisphenoid rostrum (Morel de Glasville, 1876, 1880).

In some thalattosuchians, such as *Teleosaurus* (Fig. 2B), *Steneosaurus* (Eudes-Deslongchamps, 1869), *Pelagosaurus* and *Mystriosaurus*, the postorbital bar has a particular shape. The lateral margin of the supratemporal fenestra is strongly lateroventrally bent, such that the postorbital covers the lateral margin of the jugal. The postorbital bar is thus indistinct from the dorsolateral margin of the postorbital (Fig. 6A). In metriorhynchids, a true postorbital bar exists, distinctly from the dorsolateral margin of the postorbital, and inserted medially on the jugal (Fig. 6C, D). The postorbital forms most of the bar, but does not cover the lateral margin of the jugal (Eudes-Deslongchmaps, 1869; Andrews, 1913; Schroeder, 1922; Broili, 1932; Gasparini and Chong Diaz, 1977; Gasparini et al., 2005). The postorbital bar is such distinct in *Metriorhynchus*, *Geosaurus*, *Enaliosuchus*, and *Dakosaurus*, and a lateral wing of the postorbital overhang the bar. An 'intermediate' morphology is observed in *Teleidosaurus calvadosi* (Eudes-Deslongchamps, 1869), where the postorbital bar is distinct, but the postorbital overhang is absent (Fig. 6B).

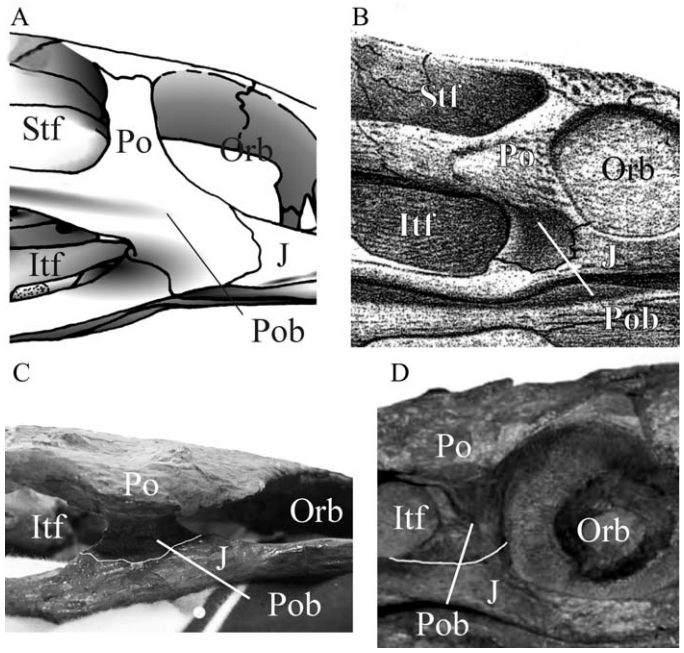

FIGURE 6. Comparison of the postorbital bar of various thalattosuchians. **A**, *Teleosaurus cadomensis*; **B**, *Teleidosaurus calvadosi* (Eudes-Deslongchamps, 1869); **C**, *Metriorhynchus superciliosus*, MNHN 1908-6; **D**, *Dakosaurus andinensis* (Gasparini et al., 2005). **Abbreviations**: **Itf**, infratemporal fenestra; **J**, jugal; **Orb**, orbit; **Po**, postorbital; **Pob**, postorbital bar; **Stf**, supratemporal fenestra.

Phylogenetic Analysis

Method—Three hundred forty-three morphological characters (Appendix 1; Supplementary Data, www.vertpaleo.org/publications/JVPContent.cfm) and 75 taxa (Appendix 2; Supplementary Data, www.vertpaleo.org/publications/JVPContent.cfm) are considered in the present cladistic analysis. The characters are those used in Jouve et al. (2006), but many have been modified, and 109 were added (Appendix 1; Supplementary Data, www.vertpaleo.org/publications/JVPContent.cfm). Twenty-eight taxa were also added to the first analysis (Appendix 2; Supplementary Data, www.vertpaleo.org/publications/JVPContent.cfm). Heuristic searches were performed using PAUP (version 4.0b10; Swofford, 2002), Winclada (version 1.00.08; Nixon, 2002), and Nona (version 2; Goloboff, 1999), with the addition sequence randomized (100,000 replications with Nona, and 500 with PAUP). All characters states were treated as unordered.

The aims of the present analysis are to test the relationships of the thalattosuchians with other crocodyliformes, and to test the relationships of main thalattosuchian taxa. Because species-level taxonomy among thalattosuchians is unclear, only taxa with visibly different morphology were applied. It is especially true for *Steneosaurus*, which, as noted by Vignaud (1995), has a particularly variable morphology. Three different morphologies have been selected. For '*Mystriosaurus*,' the specimen used is that referred by Telles-Antunes (1967) as *Mystriosaurus* cf. *bollensis*. '*Steneosaurus larteti*' is based on the specimen described by Eudes-Deslongchamps (1869; pl. XIV); and '*S. bollensis*' is based on the specimens described by Westphal (1961, 1962), SMNS10985, NHM R756, and an uncatalogued NHM specimen.

Thalattosuchians within Crocodylomorpha—Four equally most parsimonious trees with a length of 1462 steps (C.I. excluding uninformative characters: 0.28; R.I.: 0.66) were generated both with PAUP and Nona (Fig. 7A).

Herein, as in many analyses (Wu et al., 1997, 2001; Buckley and Brochu, 1999; Ortega et al., 2000; Larsson and Gado, 2000; Brochu et al., 2002; Pol, 2003; Jouve, 2004; Pol and Norell, 2004a, b; Pol et al., 2004; Pol and Apesteguia, 2005; Gasparini et al., 2005; Jouve et al., 2006), Thalattosuchia is included in Neosuchia, forming a 'longirostrine clade' with Dyrosauridae and Pholidosauridae, whereas it is a primitive mesoeucrocodylian in many other studies (Buckley et al., 2000; Sereno et al., 2001, 2003; Tykoski et al., 2002; Turner and Calvo, 2005). If the thalattosuchians are forced to be basal mesoeucrocodylians, the consensus tree is 26 steps longer. If, however, the characters most frequently suggested to be dependent on the longirostrine morphology are excluded from the analysis (5, 7, 8, 12, 15, 30, 46, 47, 68, 83, 103, 150, 161, 172, 189, 247, 284, 297, 337), the thalattosuchians are the sister taxon of all other crocodyliformes. This solution is not the best way to test the phylogenetic analysis of the crocodyliformes, as the characters deleted should be informative for the relationships of other taxa. If other than metriorhynchid thalattosuchians (the longirostrinemost thalattosuchians) are deleted from the analysis, Thalattosuchia is basal to other mesoeucrocodylians in the consensus tree, and relationships strongly differ from the first result (Fig. 7B). In this case, if the thalattosuchians are forced to be the sister taxon of the clade formed by the pholidosaurids, dyrosaurids and *Elosuchus*, the consensus tree is 27 steps longer. This result is not found if only the basalmost thalattosuchians, which are also part of the most longirostrine forms, are retained (*Teleosaurus* and *Peipehsuchus*). This solution is also problematic, as the most primitive thalattosuchians are deleted, the most primitive condition of the characters found in this taxon is also deleted, and this can introduce bias in the analysis.

These results clearly suggest a dependence of the derived phylogenetic position as neosuchians of the thalattosuchians with their longirostrine condition, but it is difficult to provide a

FIGURE 7. Phylogenetic relationships of Crocodyliformes. **A**, the strict consensus of the four most parsimonious trees of Crocodyliformes found based on a cladistic analysis of 75 taxa and 343 characters (Appendices 1, 2, and Supplementary Data, www.vertpaleo.org/publications/JVPcontent.cfm), tree length: 1462 steps long (C.I. excluding uninformative characters: 0.28; R.I.: 0.66); B, the strict consensus of the 67 most parsimonious tree of Crocodyliformes found based on a cladistic analysis if *Teleosaurus*, *Peipehsuchus*, '*S. bollensis*,' *Pelagosaurus*, '*S.larteti*', '*Mystriosaurus*,' *T. calvadosi*, '*T.*' *bathonicus*, and '*T.*' *gaudryi* are deleted from the analysis (Appendices 1, 2, and Supplementary Data, www.vertpaleo.org/publications/JVPcontent.cfm), tree length: 1372 steps long (C.I. excluding uninformative characters: 0.29; R.I.: 0.63).

satisfactory solution to this problem. If the most longirostrine thalattosuchians or 'longirostrine characters' could be deleted from the analyses, these involve loss of information. Until the characters to be dependent of the longirostrine morphology was not clearly identified (that is not the case for characters cited above), this problem will persist. As the deletion of the most longirostrine thalattosuchians precludes the longirostrine problem in the phylogenetic analysis of Crocodyliformes, this deletion, at the moment, seems to be the less unsatisfactory solution to assess the crocodyliform relationships.

Thalattosuchian Relationships—Vignaud (1995), provided a 'hand-made' cladogram, but did not use a computer-based method, whereas Gasparini et al. (2005) included eight species, mainly metriorhynchids. Until now, the most complete phylogenetic analysis on thalatosuchians was proposed by Mueller-Töwe (2005, 2006), including 25 thalattosuchians. All other previously cited studies used Metriorhynchidae, Teleosauridae, and *Pelagosaurus*. The present work includes fourteen thalattosuchian species.

Teleosauridae traditionally groups *Teleosaurus* and *Steneosaurus* (see Vignaud, 1995, for a complete review). *Pelagosaurus* was considered as a teleosaurid, but several authors have seen this species as more closely related to the metriorhynchids (Mercier, 1933; Buffetaut, 1980a, b; Vignaud, 1995). In most cladistic analyses, *Pelagosaurus* is the basal-most thalattosuchian (Benton and Clark, 1988; Clark, 1994; Wu et al., 1997, 2001; Buckley and Brochu, 1999; Buckley et al., 2000; Larsson and Gado, 2000; Brochu et al., 2002; Tykoski et al., 2002; Pol, 2003; Pol and Norell, 2004a, b; Pol et al., 2004; Pol and Apesteguia, 2005; Turner and Calvo, 2005). Gasparini et al. (2005) and Mueller-Töwe (2005, 2006) are the first to consider *Pelagosaurus* as more closely related to *Steneosaurus* than to other thalattosuchians in a cladistic analysis. Pierce and Benton (2006), reconsidering the characters used in these analyses, concluded that further investigations were required to clarify the *Pelagosaurus* relationships.

In the present work, *Pelagosaurus* forms an unresolved clade with '*S. larteti*' at the base of the metriorhynchids + '*Mystriosaurus*' clade (Fig. 7A). In the trees, *Pelagosaurus* is alternatively closely related to *Steneosaurus larteti*, or to metriorhynchids + '*Mystriosaurus*'. So, the teleosaurids are paraphyletic, and *Pelagosaurus* is not the basal-most thalattosuchian. *Teleosaurus* is the basal-most thalattosuchian, and *Peipehsuchus* is more closely related to other thalattosuchians than to *Teleosaurus*. The assemblage of three species, often considered as *Steneosaurus*, '*S. bollensis*,' '*S. Larteti*,' and '*Mystriosaurus*' cf. *bollensis*, is polyphyletic. As the taxonomy of this genus is not clear, and as all species have not been included herein, this latter result needs further research.

These results consistently differ from this obtained by Mueller-Töwe (2005, 2006), where *Pelagosaurus* is the most basal Teleosauridae, and *Teleosaurus* a teleosaurid more closely related to *Steneosaurus megarhinus* rather than to other taxa. Herein, considering only the thalattosuchians, several outgroup combinations have been analyzed, to test their influence on the thalattosuchian relationships. If *Postosuchus*, *Dibothrosuchus*, and *Sphenosuchus* are retained as outgroups, the thalattosuchian relationships strongly differ (Fig. 8A), and if *Dyrosaurus* and *Pholidosaurus* are added, the result differs from both the previous ones (Fig. 8B). In the second analysis, both *Pelagosaurus* and *Teleosaurus* have the same distribution in the tree as proposed by Mueller-Töwe (2005, 2006). All other tested combinations do not differ from the result presented here (Fig. 7A) (protosuchians, notosuchians and goniopholidids used as outgroups). Thus, the outgroups used consistently influence the tree topology and the thalattosuchian relationships proposed by Mueller-Töwe (2005, 2006) are probably related to the outgroups chosen for this analysis.

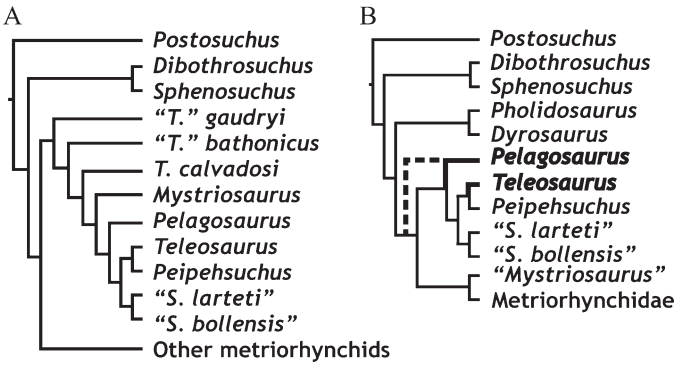

FIGURE 8. Simplified trees of the thalattosuchian relationships obtained with various outgroups. **A**, tree obtained with *Postosuchus*, *Dibothrosuchus*, and *Sphenosuchus* as outgroups (tree length: 296 steps long); **B**, with *Postosuchus*, *Dibothrosuchus*, *Sphenosuchus*, *Dyrosaurus*, and *Pholidosaurus* as outgroups (tree length: 393 steps long). In dashed line: alternative relationships of *Pelagosaurus*.

Moreover, possible dependence of parsimony analyses on snout shape with the present matrix appears not to influence relationships among thalattosuchians. If the characters related to the longirostrine morphology are deleted (see above), differences are weak: '*S. bollensis*' and *Peipehsuchus* are sister taxa, more closely related to the metriorhynchids than to other thalattosuchians.

Metriorhynchidae traditionally includes *Metriorhynchus*, *Geosaurus*, *Enaliosuchus*, *Teleidosaurus*, and *Dakosaurus*. Gasparini et al. (2005) included two *Metriorhynchus*, two *Geosaurus*, and two *Dakosaurus*, while Mueller-Töwe (2005, 2006) included two *Teleidosaurus*, one *Dakosaurus*, four *Geosaurus* and three *Metriorhynchus* species in their cladistic analyses. Both have results congruent with the relationships presented herein. In the present analysis, the metriorhynchids form a clade, where *Enaliosuchus* is more closely related to *Dakosaurus* than *Geosaurus*; *Metriorhynchus* is more closely related to previous clade than to *Teleidosaurus*, this latter being paraphyletic and the basal-most metriorhynchid (Fig. 7A). These relationships were also provided by previous authors, without the use of the cladistic method, such as Vignaud (1995) and Buffetaut (1980a, b). Schroeder (1922) and Hua et al. (2000) considered *Enaliosuchus* as closely related to *Geosaurus*. Herein, this species is more closely related to *Dakosaurus*, a relationship supported by three synapomorphies: a shorter rostrum [7(1)], a short distance between the nasal and the anterior margin of the supratemporal fenestra [312(1), convergent with '*T.*' *gaudryi*], and the posterior process of the prefrontal that reaches the anterior margin of the supratemporal fenestra. *Teleidosaurus* was first considered as a basal metriorhynchid by Collot (1905), a hypothesis supported latter by Mercier (1933) and Buffetaut (1980), the latter considering the three species as three 'grades' from *Pelagosaurus* to *Metriorhynchus*. This hypothesis is confirmed here, as *Teleidosaurus* is paraphyletic, the characters traditionally recognised as metriorhynchids being 'progressively acquired' by the three species. In node 6 (Fig. 7A), the postorbital bar is distinct from the dorsolateral margin of the postorbital [72(1), 258(1)], when it is indistinct in other thalattosuchians. This distinct postorbital bar observed in the metriorhynchids is obtained by the 'formation' of a lateral concavity in the bar, from its posterior to its anterior portion. An intermediate morphology is seen in *Teleidosaurus calvadosi*, where the concavity is only present in the posterior portion of the bar. '*T.*' *bathonicus* is more closely related to other metriorhynchids than *T. calvadosi*, a relationships supported by the lacrimal orbital contour that is facing laterally [51(1)]. '*T.*' *gaudryi* and more derived metriorhynchids are

supported by the participation of the nasal to the antorbital fenestra [251(1)], the prefrontal penetrating the nasal posteriorly [254(1)], and the lacrimal exceeding the anterior margin of the antorbital fenestra [314(0)]. All these characters are found in all other metriorhynchids. So, as reported by previous authors (Mercier, 1933; Buffetaut,1980a, b), *Teleidosaurus* represents intermediate morphology between 'teleosaurs' and more derived metriorhynchids, where the characters appeared in *Teleidosaurus* are strongly exaggerated in more derived taxa, such as the presence of a true postorbital bar with a lateral wing, the lacrimal completely lateral, and the prefrontal strongly penetrating the nasal posteriorly.

The present phylogenetic analysis also allows us to test homology of the paranasal cavity and antorbital fossa in these taxa. As the paranasal cavity is absent in *Metriorhynchus*, Witmer (1997) suggested that the 'internalisation' of the antorbital fossa (to form the paranasal cavity) was present in *Pelagosaurus* convergently with other crocodyliformes where this cavity is 'internalised', such as crocodylians. The antorbital fossa is absent in *Teleosaurus*, '*S. bollensis*', *Pelagosaurus*, '*S. larteti*', and '*Mystriosaurus*'. As *Metriorhynchus* is more derived than all these taxa (Fig. 7A), the absence of an antorbital fossa is a primitive condition in thalattosuchians, and its presence observed in *Metriorhynchus* is thus a reversed condition. An 'intermediate' stage is observed in *Teleidosaurus* (Witmer, 1997), where a shallow and short groove is present anterior to the antorbital fenestra. The anterior groove observed in *Metriorhynchus* is probably not the homologue structure of the antorbital fossa, but more probably a new structure. The absence of the paranasal cavity is the consequence of the medial concavity of the lateral wall of the chamber due to the presence of the external maxillary groove, closing the internal chamber. In *Metriorhynchus*, the chamber is closed, but not reopened externally as suggested by Witmer (1997), the external groove being a new structure. This is also suggested by the presence of the two structures, a small external groove and a paranasal cavity in *Pelagosaurus*. *Teleidosaurus*, with its lateral groove more developed than in *Pelagosaurus*, would have a smaller paranasal cavity. The nasal salt gland being hypertrophied in *Geosaurus*, the external groove was interpreted as possibly used to allow the drainage of the salt glands (Fernandez and Gasparini, 2000). The appearance of this structure could be related to the size of the salt gland, also related to the better adaptation of metriorhynchids to the marine life. This increasing of the adaptation to a marine mode of life is also observed in postcranial skeleton, as the ventral and dorsal armor is lost, the limbs are weaker and spatulate, and the tail is 'fish-shaped.'

Conclusion

The morphology of the nasal cavity, and related foramina such as paranasal cavity and maxillary neurovasculature, differs between *Teleosaurus*, *Pelagosaurus*, and *Metriorhynchus*. As the condition is unknown in other thalattosuchians, and in many crocodyliforms, this character cannot be used in phylogenetic analyses. The nasal cavity needs thus more investigation, at least in thalattosuchians, where the morphologic difference could have a phylogenetic significance.

In the phylogenetic analysis provided herein, the relationships of Thalattosuchia with other crocodyliformes remains problematic, as the longirostrine morphology induces bias in the result. Deletion of the most longirostrine thalattosuchians, considerably changes the results, and the thalattosuchians have a basal position, more consistent with the traditional view. As a temporary solution, use of the less longirostrine thalattosuchians in the phylogenetic analyses should be the less unsatisfying solution.

The thalattosuchian relationships provided herein strongly differs from the previous results, particularly in *Pelagosaurus* and *Teleosaurus* relationships. Previous analyses including numerous thalattosuchians seem to have their results strongly correlated to the chosen outgroups. Here, the teleosaurids are paraphyletic, and *Teleosaurus* is the basal-most thalattosuchian. More investigations are required to highlight the relationships of *Steneosaurus*, and *Metriorhynchus*, as these genera have particularly unclear taxonomy, and very different morphologies between their respective species. The next step would be to clarify the taxonomy of these genera, and to break down the study in small OTU, including more species. To avoid the outroup problem described above, several outgroups should be successively tested for these OTU. Several currently recognized genera may not be monophyletic.

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APPENDIX 1. The characters used in the present analysis proceed from various works.
They are from or modified from Gasparini et al. (1991), Gasparini et al. (1993), Gomani (1997), Buckley and Brochu (1999), Ortega et al. (2000), Buckley et al. (2000), Wu et al. (2001) (mainly inspired from Benton and Clark, 1988), Sereno et al. (2001), Tykosky et al. (2002), Sereno et al. (2003), Martinelli (2003), Pol (1999, 2003), Rogers (2003), Pol et al. (2004), Pol and Norell (2004a, b), Jouve (2004), Pol and Apesteguia (2005), Gasparini et al., 2005, and Jouve et al. (2006). 49 characters are new. All characters are treated as unordered.
(1) Ornamentation of external surface of frontal and parietal: smooth (0); formed by grooves and ridges (1); or with circular or subpolygonal pits (2). [Modified from Wu et al., 2001a (1), Ortega et al., 2000 (1), and Jouve, 2004 (1)].
(24) Posterior margin of the external nares formed by the premaxilla gently curved (0) or presence of a posterior notch in the premaxilla (1). [Modified from Pol, 1999, 2003 (135 and 123 respectively)].
(34) Direction of premaxillo-maxillary suture in palatal view: cranially directed (0), sinusoidal, posteromedially directed on its lateral half and anteromedially directed along its medial region (1), caudally directed (2), or perpendicular to the longitudinal axis of the skull (3). (Direction of suture is evaluated with respect to a theoretical line that passes between the lateral contact of both bones). [Modified from Ortega et al., 2000 (9), Pol and Norell, 2004 (126)].
(35) Ventral edge of premaxilla with respect to ventral edge of maxilla in lateral view: placed almost at same height or premaxilla ventrally offset (0); ventral margin of rostrum strongly dorsally convex at the level of the premaxillary-maxillary suture (ventralmost margin of premaxilla at same height as the ventralmost margin of the maxilla), and an-terior dorsal contour of dentary is also strongly concave (1). [Modified from Ortega et al., 2000 (10)].
(48) Nasal sends a small anterolateral process between maxilla and premaxilla (0) or premaxilla-maxilla suture straight, continuous with the nasal-maxilla suture (1). [Modified from Pol, 1999, 2003 (140 and 127 respectively)].
(65) Jugal does not exceed the anterior margin of the orbit (0), exceeds slightly (1), or exceeds strongly, such as the anterior process of jugal, from its anteriormost participation to the orbit to its anterior tip, is nearly as long as or longer than the orbital length (2). [Modified from Pol, 1999, 2003 (134 and 122 respectively)].
(73) Base of postorbital process of jugal directed posterodorsally (0), dorsally (1), or anterodorsally (2). [Pol, 1999, 2003 (156 and 142 respectively)].
(88) Parietal without broad occipital portion (0), or with broad parietal occipital portion as or nearly as high as the supraoccipital exposure (1). [Modified from Wu et al., 2001a (32)].
(91) Parieto-postorbital suture: absent (0), present but not on dorsal surface of skull roof (1); present on dorsal surface of skull roof (2). [Modified from Ortega et al., 2000 (27)].
(98) Squamosal remains anterior to the quadrate condyle (0) or reaches the level (1), or extendes far posterior to the quadrate condyle (2) in lateral view. [Jouve, 2004 (90)].
(99) Unsculpted ventral projection of the squamosal enclosing the dorsal half of the paroccipital process: absent (0), present (1). (New).
(109) Supratemporal fenestra smaller or nearly same size as orbit, wider or as wide as long (0), larger than orbit, but less than twice longer than wide (1), or larger than orbit, but nearly twice longer than wide (2). [Modified from Wu et al., 2001a (131)].

(140) Mandibular condyle of quadrate positioned ventral to occipital condyle but about level of the lower tooth row (0), ventral to occipital condyle but below level of the lower tooth row (1), or placed at level with occipital condyle (2). [Modified from Wu et al., 2001a (124) and Pol and Norell, 2004 (104)].
(149) Basisphenoid smooth (0), bears a strong anteroposterior medial crest (1), bears two crests (2), or three crests (3). [Modified from Jouve, 2004 (139) and Pol, 2004 (179)].
(150) Ventral portion of basioccipital thin, without well developed bilateral tuberosities (0) or ventral portion anteroposteriorly thick, rugous, with pendulous tubera (1). [Modified from Wu et al., 2001a (57)].
(152) Ventral projection of the basioccipital ventrally indistinct (0) or distinct (1) from the exoccipital in occipital view. [Modified from Jouve, 2004 (142)].
(171) Sharp ridge along the ventral surface of angular: absent (0), or present (1). [Pol and Norell, 2004 (186)].
(174) Retroarticular process short, does not ascend to the articular glenoid cavity (0), or ascends surpassing the articular glenoid cavity (1) or extremely dorsally curved, ascends surpassing largely the articular glenoid cavity (2). [Modified from Ortega et al., 2000 (93) and Jouve, 2004 (163)].
(180) Coronoid: short (0), long, anteriorly extended (1), or absent (2). [Modified from Ortega et al., 2000 (98) and Jouve, 2004 (170)].
(181) Premaxillary tooth row orientation: arched laterally (0), angled, teeth lined posterolaterally (1), or angled, tooth lined laterally (2). [Modified from Sereno et al., 2001 (69)].
(182) Number of premaxillary teeth: five (0), four (1), three (2), or two (3). [Wu and Sues, 1996 (27); Ortega et al., 2000 (133); Pol and Norell, 2004 (105)].
(183) Number of maxillary teeth: more than twenty (0), eight to twenty (1), seven (2), six (3), five (4), or four or less teeth (5). [Modified from Pol and Norell, 2004 (107), Wu and Sues, 1996 (30) and Ortega et al., 2000 (164)].
(193) Last premaxillary tooth, position: anterior (0), anterolateral (1), or anteromedial (2) to first maxillary tooth. [Modified from Sereno et al., 2001 (70)].
(235) Posterior margin of the orbit located anteriorly to the posterior margin of the suborbital fenestra (0), or posteriorly or at the same level as the posterior margin of the suborbital fenestra (1). [Jouve, 2004 (195)].
(236) Posterior edge of the supratemporal fenestra thin (0) or thick (1). [Modified from Jouve, 2004 (184)].
(237) Supratemporal fenestra: present (0), or absent (1). [Ortega et al., 2000 (72)].
(238) Dorsal margin of the lateral edge of the supratemporal fenestra (postorbital and squamosal) nearly horizontal or slightly laterally deflected (0), or strongly laterally deflected (1). (New).
(239) Dorsal margin of the lateral edge of the supratemporal fenestra (postorbital and squamosal) ornamented (0), or smooth (1). (New).
(240) Infratemporal fenestra largely hidden from ventral view by the pterygoid flange (0), or largely visible in ventral view, laterally to the pterygoid flange (1). [Modified from Jouve, 2004 (189)].
(241) Infratemporal fenestra widely opened and nearly twice shorter than supratemporal fenestra (0), as long as supratemporal fenestra (1). (New).
(242) Anterior margin of the choanal opening: gently rounded (0), or tapers anteriorly between the palatines (1). (New).
(243) Choanal opening: opened posteriorly and continuous with pterygoid surface (0), or closed posteriorly by an elevated wall formed by the pterygoids (1). [Pol and Norell, 2004 (183)].
(244) Choanal septum shape: narrow vertical bony sheet (0), or T-shaped bar expanded ventrally (1). [Pol and Apesteguia, 2005 (186)].
(245) Flat ventral surface of internal nares septum: anteriorly broad (0), or tapering anteriorly (1). [Pol and Apesteguia, 2005 (220)].
(246) Posterior margin of the otic aperture smooth (0), or invaginate (1). [Brochu, 1999 (102)].
(247) Distance between the tip of the snout and the anteriomost position of the premaxilla-maxilla suture in dorsal view is larger (0), or smaller (1) than the distance between the anteriormost position of premaxilla-maxilla suture in dorsal view and the posterodorsal extremity of the premaxilla. [Jouve, 2004 (205)].
(248) Absence (0) or presence (1) of two foramina in the palatal surface in the premaxillae-maxillae suture (no pits for dentary teeth). (New).
(249) Edge of the maxillary tooth alveoli lower or at the same level than the space between toothrow (0), or edge of the maxillary tooth alveoli higher than the space between toothrow (toothrow underline) (1). [Hua and Jouve, 2004 (165)].
(250) Posterior process of ventral lamina of maxilla without tooth short (0), or long (1). (New).
(251) Nasal participation in antorbital fenestra: yes (0), or no (1). [Ortega et al., 2000 (70)].
(252) Nasal lateral edges from its posteriormost contact with the maxilla to the posteriormost contact with the external nares if exists, or the anterior tip of nasal: nearly parallel (0), parallel but the anterior end oblique to each other (1), or entirely oblique to each other (2). [Modified from Pol, 1999 (141); Pol and Norell, 2004 (128)].
(253) Posterolateral region of nasals: flat surface facing dorsally (0), or lateral region deflected ventrally, forming part of the lateral surface of the snout (1). [Pol and Apesteguia, 2005 (223)].
(254) Prefrontal contact nasal along medial edge only (0), or penetrates the nasal anteriorly, separating the nasal in a posteromedial and a posteroventral process (1). (New).
(255) Lateral margin of prefrontal continuous with the laterodorsal margin of the orbit formed by the frontal (0), or laterally expended, forming a lateral "lobe" over the orbit (1). (New).
(256) Dorsal margin of orbit in dorsal view rounded or forms widely opened and gently rounded "V" (0), or forms acute and narrow "V" (1). (New).
(257) Anterolateral postorbital process absent or small (0), or contacts the dorsal margin of the jugal (1). [Jouve, 2004, 2005 (9 and 4 respectively)].
(258) Postorbital bar: distinctive from the dorsolateral margin of the postorbital (0), or dorsolateral margin of postorbital and postorbital bar not distinctive (1). (New).
(259) Postorbital bar visible in dorsal view (0), or vertical and not visible in dorsal view (1). [Modified from Jouve, 2004 (192)].
(260) Dorsoventral height of jugal antorbital region respect to infraorbital region: equal or lower (0), or jugal antorbital region 1.5 time more expanded than minimal height of the jugal below the orbit (1). [Modified from Pol and Norell, 2004 (130)].
(261) External surface of ascending process of jugal: exposed laterally (0), or exposed posterolaterally (1). [Pol and Norell, 2004 (182)].
(262) Ventral margin of jugal between ventral contact with maxilla and quadratojugal: straight (0), or strongly arched dorsally (1). [Modified from Pol and Norell, 2004 (179)].
(263) Longitudinal ridge on lateral surface of jugal below infratemporal fenestra: absent (0), or present (1). [Pol and Norell, 2004 (183)].
(264) Posterolateral end of quadratojugal: acute or rounded, tightly overlapping the quadrate (0), or with sinusoidal ventral edge and wide and rounded posterior edge slightly overhanging the lateral surface of the quadrate (1). [Pol and Norell, 2004 (180)].
(265) Anterior process of the frontal extending far anteriorly (0), or slightly anteriorly, at the same level or posteriorly (1) to the anterior margin of the orbits. [Jouve, 2004 (178)].
(266) Width does not differ abruptly along interfenestral bar (0), or anterior portion (frontal) much wider than posterior portion (parietal) (1). (New).
(267) Angle between posteromedial process (interfenestral bar) and lateral process of jugal (posterodorsal margin of orbit) in dorsal view: nearly 90° (0), or much less than 90° (1). (New).
(268) Frontal-postorbital suture in the skull table (anterior to the supratemporal fenestra), straight (0), V shaped, frontal tapers laterally, sending a lateral process within the postorbital on the skull table (1). (New).
(269) Parietal with (0), or without (1) broad parietal occipital portion separated in two part by supraoccipital. [Modified from Wu *et al*., 2001a (32)].
(270) Parietal does not extends well into supratemporal fenestra, or when it extends, parietal does not form a long and thin anterior process between the frontal and laterosphenoid (0), or parietal extends anterolaterally, forms a long and thin anterior process between the frontal and laterosphenoid, and participates to the anteroventral margin of the supratemporal fenestra, below the frontal within the fenestra (1). (New).
(271) Dorsal surface of posterolateral region of squamosal: without ridges (0), or with three curved ridges oriented longitudinaly (1). [Pol and Norell, 2004 (184)].
(272) Posterolateral edge of squamosal: without descending ornamented process (0), or with descending ornamented process (1). [Pol and Norell, 2004 (163)].
(273) Exoccipital visible in lateral view between squamosal and quadrate, or participates to the posterior margin of the external otic aperture (0), or quadrate and squamosal sutured posterior to the external ear, and exoccipital excluded from posterior margin (1). [Modified from Jouve, 2004 (121)].

(274) Lateral edge of the skull table at the level of the postorbital-squamosal suture situated laterally at the same level (0), or medially (1) to the quadrate condyle for the jaw articulation in dorsal view. [Jouve, 2004 (170)].
(275) Maxilla-palatine suture tapers anteriorly (0), palatine anteromedially straight, perpendicular to the longitudinal axis of the skull (1), or palatine invaginated (2). [Modified from Turner and Calvo, 2005 (122)].
(276) Palatine-pterygoid contact on palate: palatines overlie pterygoids (0), or palatines firmly sutured to pterygoids (1). [Pol and Norell, 2004 (165)].
(277) Posteriorly facing notch between the base of the pterygoid wings: absent (0), present (1). [Pol, 1999 (164); Pol and Norell, 2004 (148)].
(278) Ectopterygoid medial process: single (0), or forked (1). [Ortega et al., 2000 (146)].
(279) Ectopterygoid does not connect or connect slightly the palatal branch of maxilla (0), ectopterygoid extensively connects the maxilla, but suture lateromedialy oriented (1), or anterior process of ectopterygoid long, and extensively connects the palatal branch of maxilla (2). (New).
(280) Anterior process of pterygoid ramus of quadrate do not suture (0) or sutured to the pterygoid (1). (New).
(281) Quadrate major axis directed: posteroventrally (0), ventrally or anteroventrally (1). [Modified from Pol, 1999 (166); Pol and Norell, 2004 (150), modified from Ortega et al., 2000 (44)].
(282) Orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: ventrally (0), or ventrolaterally (1). [Pol and Norell, 2004 (181)].
(283) Cross section of distal end of quadrate: mediolaterally wide and anteroposteriorly thin (0), or sub-quadrangular (1). [Pol and Norell, 2004 (164)].
(284) Basisphenoid rostrum short (0), or extremely long anteriorly (1). [Jouve, 2005 (2)].
(285) Basisphenoid-pterygoid suture nearly straight transversely (0), or basisphenoid tapers anteriorly between the two pterygoids (1). (New).
(286) Absence (0) or presence (1) of a medial crest on the posterior surface of the ventral process of the basioccipital. [Modified from Jouve, 2004 (185)].
(287) Posterior surface of basioccipital ventral to the occipital condyle short and gently curved, lower than the occipital condyle (0), or long, flat and nearly vertical, at least as high as occipital condyle (1). [Modified from Jouve, 2004 (197)].
(288) Absence (0), or presence (1) of a deep medial depression ventrally to the basioccipital and posteriorly to the medial eustachian foramen. [Jouve, 2004 (198)].
(289) Palpebrals: separated from the lateral edge of the frontals (0), or extensively sutured to each other and to the lateral margin of the frontals (1). [Pol and Norell, 2004 (181)].
(290) Dorsal surface of mandibular symphysis: flat or slightly concave (0), or strongly concave and narrow, trough shaped (1). [Pol and Apesteguia, 2005 (184)].
(291) Dorsal edge of dentary: straight (0), or showing a single concave arch behind the caniniform tooth (1), edge sinusoidal, with two concave waves (2). [Modified from Ortega et al., 1996 (1)].
(292) Ventral exposure of splenials: absent (0), or present (1). [Ortega et al., 1996 (9)].
(293) Splenial: thin posterior to symphysis (0), or splenial robust dorsally posterior to symphysis (1). [Ortega et al., 1996 (7)].
(294) Posterior peg at symphysis: absent (0), or present (1). [Pol and Apesteguia, 2005 (181)].
(295) Lateral surface of the anterior region of surangular and posterior region of dentary: without a longitudinal depression (0), or with a longitudinal depression (1). [Ortega et al., 1996 (5)].
(296) Longitudinal ridge along the dorsolateral surface of surangular: absent (0), or present (1). [Pol and Norell, 2004 (187)].
(297) Robust and short teeth, with wide alveoli (0), or thin and long teeth (1). [Modified from Jouve, 2005 (11)].
(298) Distal portion of humeral shaft rounded (0), or flattened (1) in cross section. (New).
(299) Illium: large, longer than high (0), small, higher than long (1). (New).
(300) Anteroposterior development of neural spine in axis: well developed covering all the neural arch length (0), or poorly developed, located over the posterior half of the neural arch (1). [Pol, 1999 (168); Pol and Norell, 2004 (152)].
(301) Prezygapophyses of axis: not exceeding anterior edge of neural arch (0), or exceeding the anterior margin of the neural arch (1). [Pol, 1999 (169); Pol and Norell, 2004 (153)].
(302) Sacral ribs short, robust, and slightly bent lateroventrally (0), or long, gracile, and strongly bent ventrally (1). (New).
(303) Height of neural arch of caudal vertebrae: less than two time length of centrum (0), or more than two time length of centrum (1). (New).
(304) Posterior portion of tail straight (0), or bent ventrally, tail being "fish-shaped". (New).
(305) Cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements: absent (0), or present (1). [Pol and Norell, 2004 (189)].
(306) Appendicular osteoderms: absent (0), or present (1). [Pol and Norell, 2004 (190)].
(307) Dorsal surface of osteoderms ornamented with anterolaterally and anteromedially directed ridges (fleur de lys pattern of Osmolska et al., 1997): absent (0), or present (1). [Pol and Norell, 2004 (188)].
(308) Presence of dorsal shield (0), absence of both dorsal and ventral shield. (New).
(309) External nares in dorsal view: much wider than long (0), nearly as wide as long (1), or much longer than wide (2). (Modified from Vignaud, 1995).
(310) Orbit more circular in lateral aspect (0), or in dorsal aspect (1). (New).
(311) Maximal width of the nasal less or nearly as wide as (0), wider (1), or more than twice wider (2) than the minimal width of the snout. (New).
(312) Distance between the posterior processes of nasals shorter (0) or nearly as long as the distance from posterior process of nasal to the anterior margin of the supratemporal fenestra (1). (New).
(313) Lacrimal participates to the dorsal margin of the antorbital fenestra (0), participates to the posterior margin only (1). (New).
(314) Lacrimal does not exceed (0), or exceeds the anterior margin of the antorbital fenestra (1). (New).
(315) Lacrimal visible (0) or not visible (1) in dorsal view. (New).
(316) Posterior process of prefrontal does not reach (0) or reaches (1) the level of the anterior margin of the supratemporal fenestra. (New).
(317) Anterior tip of the prefrontal reaches or exceeds (0), or remains posterior (1) to the posterior margin of the antorbital fenestra. (New).
(318) Jugal does not exceed (0) or exceeds (1) the lacrimal anteriorly. (New).
(319) Absence (0) or presence (1) of a transverse frontal ridge. (New).
(320) Absence (0) or presence (1) of a wide frontal plate in the anteromedial corner of the supratemporal fenestra. (New).
(321) Parietal widely exposed, much wider than the supraoccipital (0), or without broad occipital portion, or nearly as wide as the supraoccipital (1). (New).
(322) Short lateroventral extension of the exoccipital (0), or exoccipital covers strongly the dorsal surface of caudal branch of quadrate (1). (New).
(323) Posterodorsal margin of the skull roof not strongly W-shaped (0), or sigmoidal, strongly W-shaped, and the dorsal margin of the supraoccipital is much higher than the dorsal margin of the squamosal in posterior view (1). (New).
(324) Absence (0) or presence of a pterygoid-ectopterygoid fenestra (1). (New).
(325) Ventrally exposed part of basisphenoid: wider than long (0), longer than wide (1). (New).
(326) Medial margin of the orbit in dorsal view: formed mostly by the frontal (0), or mostly by the prefrontal, the frontal is excluded or participates only slightly (1). (New).
(327) Third dentary tooth smaller than the fourth, and alveoli separated (0), third and fourth dentary alveoli nearly equal in size, and nearly confluent (1). (New).
(328) Length of the humerus more than two-third (0), nearly two-third (1), or nearly one-third (2) the length of the femur. (New).
(329) Humerus much higher than scapula (0), or lower or nearly as long as scapula (1). (New).
(330) Ulna nearly as long as humerus (0), or more than one-quarter shorter than humerus (1). (New).
(331) Basisphenoid not or slightly visible (0), or widely exposed (1) below the basioccipital in occipital view. (New).
(332) Ventral half of the lacrymal: extending ventroposteriorly widely contacting the jugal (0), or tapering ventroposteriorly, does not contact or contacts the jugal only slightly (1). [Pol and Apesteguia, 2005 (224)].

(333) Ectopterygoid projecting medially on ventral surface of pterygoid flanges: barely extended (0), or widely extended covering approximately the lateral half of the ventral surface of the pterygoid flanges (1). [Pol and Apesteguia, 2005 (230)].
(334) Posterior teeth with rings of ondulated enamel: absent (0), or present (1). [Gasparini et al., 2005 (250)].
(335) Enlarged foramen at anterior end of surangular groove: absent (0), or present (1). [Gasparini et al., 2005 (245)].
(336) Foramen for the internal carotid artery: reduced, similar in size to the openings for cranial nerves IX-XI (0), or extremely enlarged (1). [Gasparini et al., 2005 (248)].
(337) Sculpture in external surface of rostrum: absent (0), or present (1). [Gasparini et al., 2005 (252)].
(338) Prefrontal and lacrimal around orbits: forming flat rims (0), or evaginated, forming elevated rims (1). [Gasparini et al., 2005 (256)].
(339) Nasal bones: paired (0), or partially or completely fused (1). [Gasparini et al., 2005 (257)].
(340) Medioventral projection of exoccipital remains far (0), or nearly reaches (1) the ventral projection of the basioccipital. (New).
(341) Maximal width of premaxilae less (0), or more (1) expended than the maximal width of the rostrum at the level of the 4 or 5 alveoli. (New).
(342) Upper tooth row: forms waves in ventral view (0), or nearly straight, oriented posterolaterally, each tooth being more lateral than the immediately anterior one (1). (New).
(343) When the cranioquadrate canal is closed off anteriorly by a thin lamina: dorsal lamina of exoccipital (anterior to the cranioquadrate canal) does not suture (0), or sutures (1) the quadrate or squamosal dorsally. (New).

APPENDIX 2. Material and references used for phylogenetic analysis. They are the same as in Jouve et al. (2006), but several taxa were added: *Zaraasuchus shepardi* (Pol and Norell, 2004b); *Hemiprotosuchus leali* (Bonaparte, 1971; PVL 3829); *Edentosuchus tienshanensis* (Li, 1985; Pol et al., 2004); Kayenta *Edentosuchus* (Sues et al., 1984); *Zosuchus davidsoni* (Pol and Norell, 2004a); *Hsisosuchus dashanpuensis* (Gao, 2001); *Mariliasuchus amarali* (Carvalho and Bertini, 1999); *Uberabasuchus terrificus* (Carvalho et al., 2004); *Mahajangasuchus insignis* (Buckley and Brochu, 1999); *Trematochampsa taqueti* (Buffetaut, 1976; numerous material from the MNHN collection); *Susisuchus anatoceps* (Salisbury et al., 2003); *Montsecosuchus depereti* (Wellnhofer, 1971; Buscalioni and Sanz, 1990); *Theriosuchus guimarotae* (Schwarz and Salisbury, 2005); *Borealosuchus formidabilis* (Erickson, 1976); *Allodaposuchus precedens* (Buscalioni et al., 2001); *Rhabdognathus* (Brochu et al., 2002; Jouve, 2007; MNHN TGE 3394; MNHN TGE 3395; MNHN TGE 3331; MNHN TGE 4033; MNHN TGE 3917; MNHN TGE 4256; MNHN TGE 4360; MNHN TGE 4366; MNHN TGE 4031; MNHN TGE 3917; CNRST-SUNY–190); *Teleosaurus cadomensis* (MNHN AC 8746; Eudes-Deslongchamps, 1864, 1867–1869, 1896; Geoffroy Saint-Hilaire, 1825; Sauvage, 1874); *Peipehsuchus teleorhinus* (Li, 1993); '*S. bollensis*' (Westphal, 1961, 1962; SMNS10985; NHM R756; NHM uncatalogued specimen); '*S. larteti*' (Eudes-Deslongchamps, 1869); '*Mystriosaurus*' (Telles-Antunes, 1967); '*Teleidosaurus*' *calvadosi* (Eudes-Deslongchamps, 1869); '*Teleidosaurus*' *bathonicus* (Mercier, 1933); '*Teleidosaurus*' *gaudryi* (Collot, 1905); *Geosaurus* (Fraas, 1902; Broili, 1932); *Enaliosuchus macrospondylus* (Schroeder, 1922; Hua et al., 2000); *Dakosaurus maximus* (Fraas, 1902); *Dakosaurus andinensis* (Gasparini et al., 2005).